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Minireview

The grand design of photosynthesis: Acclimation of the photosynthetic apparatus to environmental cues

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Abstract

Dynamic acclimation of the photosynthetic apparatus in response to environmental cues, particularly light quantity and quality, is a widely-observed and important phenomenon which contributes to the tolerance of plants against stress and helps to maintain, as far as possible, optimal photosynthetic efficiency and resource utilization. This mini-review represents a scrutiny of a number of possible photoreceptors (including the two photosystems acting as light sensors) and signal transducers that may be involved in producing acclimation responses. We suggest that regulation by signal transduction may be effected at each of several possible points, and that there are multiple regulatory mechanisms for photosynthetic acclimation.

Abbreviations: FR – far-red light; LHC I, LHC II – light-harvesting chlorophyll *a/b*-protein complex of PS I and PS II, respectively; P700 – primary electron donor of PS I; Pmax – maximum photosynthetic capacity; Q_A – primary quinone electron acceptor of PS II; q_N, q_P – non-photochemical and photochemical quenching, respectively; R – red light

Introduction

Daniel Arnon never ceased to wonder at and delight in the 'grand design of photosynthesis' (Arnon 1982), be it in others' achievements in photosynthesis or his own heroic discoveries of photophosphorylation. Part of the grand design of photosynthesis involves the exquisite acclimation of the photosynthetic apparatus to ever-changing environmental stimuli. It is well established that marked modulations of the composition, function and structure of the photosynthetic apparatus occur in response particularly to light, but also to temperature and the availability of water, nutrients and CO_2. Due to the extremely limited abilities of plants to change their surroundings, these highly regulated, dynamic responses occur to make the best of whatever situation the plant is faced with. Above all, it is imperative that plants maintain an effective balance between energy supply through light-harvesting and electron transport on the one hand, and energy consumption, mainly by carbon fixation on the other, since photosynthesis drives life on earth. Coordinated interactions between light-harvesting, energy conversion, electron transport, proton translocation and carbon fixation are inextricably linked in photosynthesis in response to sudden and sustained environmental fluctuations. Short-term responses such as state transitions, protective energy dissipation and the down-regulation of PS II in response to fluctuations in irradiance, serve to minimise change due to excess light by rendering some PS IIs non-functional, while simultaneously allowing efficient use of incident irradiance (cf. Horton and Ruban 1992; Chow 1994). On the other hand long-term acclimation, mediated by multitudes of signal cascades and networks, involves the coordinated reallocation of resources to achieve and maintain, not only optimal rates of photosynthesis, but also high quantum yields under limiting light and protective strate-

gies under sustained environmental stress (Anderson and Osmond 1987; Anderson et al. 1988).

Photoreceptors, such as the phytochrome family (Quail 1991) and blue/UV-A and blue/UV-B photoreceptors (Kaufman 1993), play a vital role in the regulation of gene expression at many levels during development. They exert control over huge networks of morphological and biochemical processes, in many cases by modulating signal transduction pathways for the expression of specific genes (Thompson and White 1991). It is becoming increasingly clear, however, that both the fine-tuning of the photosynthetic apparatus and the subsequent acclimation of mature tissue to environmental fluctuations depend rather on metabolic signals, derived from the physiological state of the plant, particularly photosynthesis. Developmental and environmental cues are mediated by a myriad of signal transduction cascades that involve de novo protein synthesis, and modification of existing ones; many of these responses involve reversible kinase and phosphatase activities. Feedback from photosynthesis, via the energy storage pools of ATP and NADPH, has been suggested to modulate gene expression (Melis et al. 1985; Chow et al. 1990a). Additionally, some evidence suggests that the photosystems themselves are primary photoreceptors (Chow et al. 1990a; Kim et al. 1993a; Walters and Horton 1995c). Increasingly, evidence also favours the regulation of photosynthetic acclimation by the redox status, either of the electron pool between the photosystems (Fujita et al. 1987; Melis 1991) or of PS II (Maxwell et al. 1994, 1995). The complex coordinated interactions between the responses of photoreceptors, PS II and PS I, and metabolic responses elicited from photosynthesis itself are briefly reviewed here; although data are often confusing and sometimes contradictory, we can begin to appreciate the grand design of photosynthesis.

Light acclimation: Interactions of light quality and quantity

Light acclimation of the photosynthetic apparatus involves the coordinated allocation of resources not only to achieve and maintain optimal rates of photosynthesis, but also to function effectively under limiting and excess photons. Plants experience continually changing light quality and quantity. Light varies, not only over a wide range of intensities and spectral qualities (full sun, early morning, late evening, cloud and canopy shade), but also over vastly different time scales from short sunflecks to long-lasting canopy gaps, and seasonal variations (Anderson and Osmond 1987; Anderson et al. 1988). Moreover, a continuum of light intensity and quality is experienced from stromal to granal thylakoids within chloroplasts (Terashima 1989), to different chloroplasts within leaves, to leaves within and between species. Compared with the exposed canopy, light received in shade is a blend of very weak diffuse irradiance greatly enriched in far-red (PS I light), deficient in red and to a lesser extent in blue light, interspersed with gap sunlight or sunflecks.

Non-limiting to saturating light strategies: Shade or low light plants have more Chl *b* and more of the light-harvesting chlorophyll proteins of PS II (LHC II) and PS I (LHC I) for maximal light capture. This increase in light-harvesting components occurs at the expense of electron transport, photophosphorylation and carbon fixation components, particularly Rubisco, resulting in lower photosynthetic rates which saturate at lower irradiance. Conversely, under sun and high light, plants are limited in electron transport rather than light capture and conversion: they have greater amounts of cytochrome *b/f* complex, ATP synthase, plastoquinone, plastocyanin, ferredoxin, and more carbon fixation enzymes, to support high maximal photosynthetic rates which saturate at high irradiance (Anderson and Osmond 1987). These modulations in the composition, organization and function of the photosynthetic apparatus are so well regulated, that even the Chl *a/b* ratios of leaves are a simple index of light intensity acclimation: they are linearly related to the content of cytochrome *b/f* complex, ATP synthase and Rubisco, and inversely correlated with amounts of LHC II and LHC I (Anderson et al. 1988) and stacked membranes (Anderson and Aro 1994). Only P680 and P700 are not proportional to Chl *a/b* ratios.

Light-limiting strategy: Nevertheless both photosystems undergo acclimation: two strategies are involved. First, the amounts of LHC II and LHC I serving each reaction centre decrease with increasing irradiance. Second, the amount of PS II reaction centres relative to PS I reaction centres, i.e. the photosystem stoichiometry, is altered with varying light quantity or quality. Shade and low light plants have lower PS II/PS I ratios of 1.0–1.3, due to fewer PS II units each with larger light-harvesting antennae, while sun and high light plants with PS II/PS I ratios of 1.8–2.4, have more PS II units each with smaller light-harvesting units, relative to PS I (Anderson et al. 1988). This adaptation of the photosystem stoichiometry which is

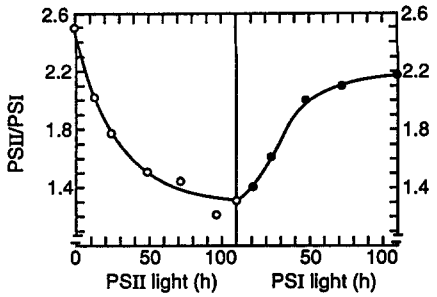

Fig. 1. The response of photosystem stoichiometry to changes in light quality during growth. Peas acclimated in PS I light (at time zero) were transferred to PS-II light and at 110 h, the same plants were transferred back to PS I light (redrawn from Melis 1991).

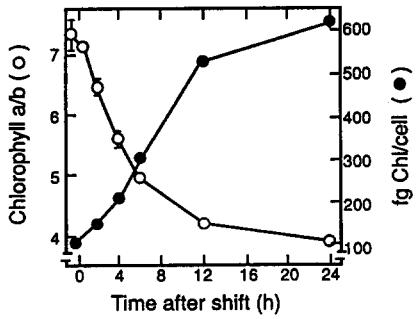

Fig. 2. Changes in the Chl content (fg Chl/cell, •) and Chl *a*/*b* ratio (o) as a function of time following transfer of an exponentially growing culture of *Chlorella vulgaris* from 5 °C to 27 °C, at constant irradiance of 150 μmol m^{-2} s^{-1} (redrawn from Maxwell et al. 1994).

influenced more by alterations of spectral quality than intensity, serves to regulate the distribution of excitation energy between the photosystems and correct any imbalances: eg plants grown in PS I light have higher PS II/PS I ratios due to increased amounts of PS II, and vice versa (Chow et al. 1990b; Melis 1991). Acclimation of plants to only light intensity or light quality demonstrates the opposing nature of regulation by quality and quantity: lower light intensity causes a decrease in PS II content on a chlorophyll basis, while the concomitant increase in PS I light in extreme shade enhances PS II content.

Acclimation also ensures that plants operate efficiently under limiting light. It is remarkable that the quantum yields of all C_3 plants are high and constant (Demmig and Björkman 1987). Measurements of quantum yields of plants grown in PS II or PS I light demonstrate that high quantum yields were obtained only when the quality of the measuring light was the same as that of the growth light (Chow et al. 1990b; Walters and Horton 1995b). This strongly suggests that modulation of the photosystem stoichiometry is a compensatory factor, along with modulations of effective light-harvesting antennae size, that ensures all plants have constant, high quantum yields at limiting light. Regulation of photosystem stoichiometry is important since most chloroplasts function for most of the time in non-saturating light, due to pronounced attenuation of light within chloroplasts, cells, leaves and canopy.

Strategies for excess photons: Acclimation is also related to the functionality and non-functionality of PS II under sudden and sustained high light stress. Plants possess many photoprotective strategies to protect PS II; particularly well studied is photoinhibition where the loss of PS II function serves to stabilize the photosynthetic apparatus in the face of photon excess (Öquist et al. 1992a,b; Anderson and Aro 1994; Osmond 1994). Irrespective of growth light acclimation, during photoinhibition more than 60% of the PS II centres remain open (Öquist et al. 1992a). This implies that all circumstances affecting the redox state of Q_A are crucially important and need to be considered: antennae size and energy distribution between photosystems, electron transport rate, light-activated zeaxanthin formation, and other mechanisms for non-photochemical dissipation of absorbed light, mainly transthylakoid pH-dependent down-regulation of PS II, cyclic events around PS II and PS I, scavenging of oxygen radicals, and more. With such cascades of varying spatiotemporal responses, plants have multiple strategies to ensure functionality of PS II (Anderson and Osmond 1987; Demmig-Adams 1990; Foyer et al. 1990; Anderson and Aro 1994; Chow 1994). The need for these processes to operate under both sudden and sustained high light stress, arises from the conflicting demands between the efficient use of light at low irradiance and protection from excess light.

Metabolic acclimation by photosynthesis

Dynamic adjustments of the photosynthetic apparatus to varying environmental stimuli are fully reversible, unless some severe stress has caused secondary effects. For example, the photosystem stoichiometry of peas grown in PSI light, on transfer to PS II light, acclimates to a comparable stoichiometry of those grown in only PS II light, and vice versa (Fig. 1; Kim et al. 1993a). *Alocasia*, often thought of as an obligate shade plant, readily adapts to full sunlight (Anderson

et al. 1988). Such dynamic changes are not restricted to light quality or quantity. The pigment composition of low temperature-grown *Chlorella* reacclimates to that of room temperature-grown cells, as described below (Fig 2; Maxwell et al. 1994). This dynamic reversibility is also true for plants stressed by high irradiance: *Dunaliella* subjected to high irradiance loses much of its chlorophyll and has a large PS II/PS I ratio of 15, due mainly to the accumulation of non-functional PS II units; on transfer to normal irradiance, the photosystem stoichiometry is restored to 1.4 (Kim et al. 1993b).

Phytochrome is not directly involved in light acclimation

To probe possible involvement of phytochrome or other photoreceptors in response to acclimation to light quality of the photosynthetic apparatus, peas were grown with brief (15 min) supplementary far-red irradiance at the end of the 12 h light period (*brief FR*), to simulate the increase of far-red light experienced in the field at the end of the day (FR/R ratio of 0.3) (Chow et al. 1990a). Compared to control plants, marked morphological changes attributable to phytochrome regulation (Smith 1982) were observed in brief FR-grown peas with an increase in internodal length, but a decrease in leaflet area, chloroplast size and chlorophyll content per chloroplast. However, brief FR had little effect on amounts of major chloroplast components (Table 1): leaf capacities for photosynthesis on a chlorophyll basis were similar, as were levels of PS II and cytochrome *b/f* complex, and activities of ATP synthase and Rubisco based on either chlorophyll or PS I content (Table 1). Relative to PS I (for which the accumulation of P700 apoprotein is known not to be regulated by phytochrome), the amounts of chloroplast components were unaffected under the same brief FR irradiance that elicited classical phytochrome-induced morphological changes, demonstrating that phytochrome exerts a negligible effect on light quality acclimation of the photosynthetic apparatus in fully-greened tissue.

Arabidopsis thaliana, grown at two light intensities of white or far-red-enriched white light, showed marked differences in Pmax, Rubisco and Chl *a/b* ratios between high and low light intensity regimes, but little response was elicited by changes in spectral quality at either light intensity, suggesting that phytochrome is not involved in light intensity acclimation (Walters and Horton 1995a).

Future use of photoreceptor-deficient mutants will greatly advance understanding of the involvement of specific photoreceptors in acclimation. Tomato mutants, deficient in phytochrome A and possibly other phytochromes, showed large increases in photosystem stoichiometry under simulated vegetation shade (enhanced PS I-light) compared to plants grown with daylight or under neutral shade (Smith et al. 1993). These results demonstrate that phytochrome A is not involved in light quality acclimation. Similarly, phytochrome-deficient *Arabidopsis* mutants were able to alter PS II/PS I ratios in response to light intensity in the same manner as wild type (Table 2; Walters and Horton 1995c), proving that phytochrome cannot be directly involved in the response to light intensity.

Photosystems II and I act as self-regulatory light sensors

To simulate extreme shade conditions, peas were grown in white light supplemented with high levels of far-red light (FR/R ratio of 0.04) (*long-term FR*), comparable to extreme shade conditions (Smith 1982). Compared to control peas, long-term FR also produced phytochrome-regulated morphological changes similar to those described above for brief FR. However, in contrast to brief FR, there was a marked increase in photosynthetic capacity on a Chl basis (Table 1), due to increased activities of Rubisco and ATP synthase and levels of Cyt *b/f* complex, and to a lesser extent PS II content, as well as a significant decrease in PS I on a chlorophyll basis. We hypothesized that the observed enhanced Pmax and chloroplast components in long-term FR was induced by far-red light acting through PS I, to increase photosynthesis by extra cyclic electron transport and/or enhanced non-cyclic electron transport due to state transitions (Chow et al. 1990a). The extra supply of ATP would then be available to regulate gene expression to increase protein synthesis, protein translocation across membranes and assembly of complexes in a post-translational manner. Thus, long-term FR induces an increase in chloroplast components (Table 1) by a feedback mechanism regulated by photosynthesis. Modulation of these energy storage pools of ATP and NADPH in the chloroplast stroma will regulate gene expression by enhanced transcription/translation and biosynthesis/assembly activities being directed towards those components of chloroplast function that are rate-limiting, as well as degradation of other components (e.g. decrease of PS I in

Table 1. Photosynthetic acclimation to brief supplementary and prolonged far-red irradiance. Peas were grown in white light (12 h light/12 h dark) without, or with supplementary far-red light for 15 min at end of 12 h photoperiod (**brief FR**), or throughout the entire 12 h light period (**long-term FR**). (Chow et al. 1990a)

		PS II	Cyt *f*	PS I	PS II/PS I	ATP	Rubisco	P_{max}
		(mmol mol Chl^{-1})				(mmol mol Chl^{-1} s^{-1})[a]		
Brief FR	+FR	1.89	0.78	1.53	1.23	353	62	41.1
	-FR	2.09	0.87	1.62	1.29	368	67	39.2
	+FR/-FR	0.90	0.89	0.94		0.96	0.92	1.05
Long-term FR	+FR	2.38	1.34	1.46	1.63	357	89	50.4
	-FR	2.21	1.11	1.78	1.24	256	70	38.5
	+FR/-FR	1.08	1.21	0.92		1.39	1.29	1.31

[a]The rates refer to inorganic phosphate liberated for ATP hydrolysis, CO_2 fixed for Rubisco activity and O_2 evolved for P_{max}.

Table 2. Acclimation of *Arabidopsis thaliana*[a] with altered photomorphogenesis to light intensity (Walters and Horton 1995b)

Genotype	Growth light (μmol m^{-2} s^{-1})	P_{max} (μmol O_2 mg Chl^{-1} h^{-1})	Chl *a/b*
Wild type	100 white	109	2.83
	400 white	360	3.52
	50 red	189	3.59
200 red	178	3.48	
hy2 hy3	50 white	125	4.51
	250 white	306	5.85
hy4	100 white	162	3.43
	400 white	344	3.95

[a]The double mutant *hy2 hy3* lacks both chromophore synthesis and the structural gene for phytochrome B, while the *hy4* mutation affects a gene believed to encode a blue light receptor.

PS I-growth light) (Melis et al. 1985, 1991; Chow et al. 1990a; Anderson and Chow 1992).

Specific involvement of blue light in adjustments of chloroplast composition

Several lines of evidence suggest that the regulation of photosystem stoichiometry involves specific detection of blue light. Surprisingly, with *Arabidopsis*, Walters and Horton (1995b) demonstrate the importance of blue light in the growth environment: (a) *Arabidopsis* grown in high and low light exhibit strong acclimation to light intensity with marked changes in maximum rates of photosynthesis and Chl *a/b* ratios (Table 2). Growth in red light, however, abolished these changes (Table 2), suggesting that a blue light/UV-A photoreceptor may be involved in acclimation to light intensity. (Contrariwise, an *hy4* mutant, lacking the gene thought to encode the blue light receptor, showed acclimation to light intensity). (b) *Arabidopsis* grown under several light environments of varying spectral quality but constant intensity, demonstrated that supplementing red light with low levels of blue light led to a large increase in PS II content, while further increase in blue had the opposite effect. The latter response was abolished by the *hy4* mutation known to affect certain blue-light receptor morphogenic events. Walters and Horton

(1995c) suggest two roles for blue light responses: a blue-high-fluence (BHF) which controls photosystem stoichiometry, and a blue-low-fluence (BLF) which is required for the activation of the response. The effects of the red light response are not easy to explain, since the BHF response was only apparent when red light was also taken into account: the more intense the background light, the greater was the blue light required to have the same effect on PS II content. They suggest that either red light may function by exerting photosynthetic control, or there may be another, as yet unidentified red light receptor involved, as Tsinoremas et al. (1994) suggest for cyanobacteria.

With peas grown in low and moderate light (20 or 200 μmol m^{-2} s^{-1}) (white, blue-enriched and red-enriched light), an increase in blue-enriched light fluence was more effective than red light in inhibiting internode growth, and enhancing the Chl *a/b* ratio: Rubisco and Cyt *f* also increased 2-fold in response to blue light (Lopez-Juez and Hughes 1995). These results are consistent also with a role for the blue light receptor in detecting low and high fluence, and thereby regulating acclimation, but Lopez-Juez and Hughes (1995) consider that the role of photosynthesis and another red photoreceptor may also be involved. Although these recent results with *Arabidopsis* and peas need to be explored further, and extended to other species, they clearly demonstrate the need to consider blue light being involved in the complex interaction between light quality and quantity.

Acclimation is influenced by metabolic responses to stimuli other than light

(i) Growth at low temperature mimics high light acclimation

While the rates of photochemical reactions are independent of temperature (Q_{10} of 1), those of enzyme-mediated reactions decline as temperature is lowered (Q_{10} of 2). Exposure of plants or algae to lower temperatures may result in the photosynthetic apparatus absorbing more light than can be readily dissipated by carbon fixation, resulting in imbalance between energy supply and consumption (Huner et al. 1993).

Recently, a compelling example of metabolic responses has been demonstrated by Maxwell et al. (1994, 1995) with *Chlorella* adapted to low temperature. *Chlorella vulgaris* cells grown at 5 °C had two-fold higher Chl *a/b* ratios, 5-fold lower chlorophyll, increased xanthophyll and decreased LHC II contents compared to cells grown at 27 °C, even though the growth irradiance was constant (150 μmol m^{-2} s^{-1}) (Maxwell et al. 1994). Moreover, the 5 °C-grown cells exhibited light-saturated rates of photosynthesis that were 2.8- and 3.9-fold as high as that of 27 °C-grown cells, measured at 27 °C and 5 °C, respectively. Steady-state fluorescence measurements showed that 5 °C-grown cells had higher q_P values. Maxwell et al. (1994, 1995) suggest that *Chlorella* acclimated to low temperature may adjust its photosynthesis in response to excitation pressure on PS II and not on absolute irradiance, and that the redox state of Q_A may act as a signal for temperature acclimation. Excitation pressure on PS II is defined as the amount of Q_A in the reduced state $Q_A$red/($Q_A$red + $Q_A$ox), and is approximately given by $(1 - q_P)$, where q_P represents photochemical quenching derived from modulated steady-state fluorescence measurements.

Additional support for the idea of excitation pressure on PS II comes from two types of transfer experiments, involving change of (i) temperature at constant irradiance and (ii) irradiance at constant temperature (Maxwell et al. 1994). Dramatic, dynamic acclimation occurred within 12 h of transfer of the 5 °C-grown cells to 27 °C (Fig. 2) such that the pigment content and Chl *a/b* ratio were similar to control 27 °C-grown cells. Growth of *Chlorella* at constant low temperature, but with a 30-fold lower light intensity (150 to 5 μmol m^{-2} s^{-1}), resulted in Chl *a/b* ratios and chlorophyll content being similar to those of cells grown at 27 °C and higher light intensity. Both transfer experiments demonstrate that acclimation to low temperature mimics high light acclimation.

Ideas on PS II excitation pressure being a critical primary signal were also tested with *Chlorella* grown under very high irradiance (Maxwell et al. 1995). *Chlorella* grown at low temperature (5 °C/150 μmol m^{-2} s^{-1}) or at very high irradiance (27 °C/2200 μmol m^{-2} s^{-1}), experienced comparable excitation pressure on PS II, with $1 - q_P$ values of 0.7, whereas *Chlorella* exposed to normal conditions (27 °C/150 μmol m^{-2} s^{-1}) or low temperature under low irradiance (5 °C/20 μmol m^{-2} s^{-1}) exhibited a much lower PS II excitation pressure of 0.1–0.2. As shown in Table 3, *Chlorella* grown under either regime at high PS II excitation pressure exhibited 3-fold higher maximum photosynthetic rates, higher Chl *a/b* ratios and lower LHC II content. Concomitantly, cells grown under the high PS II excitation regimes showed a 3- to 4-fold greater resistance to photoinhibition, than those grown under the less stressed conditions of lower PS II excitation

Table 3. Characteristics of *Chlorella vulgaris* grown under two conditions of low ans high excitation pressure of PS II (Maxwell et al. 1995)

	Growth temperature (°C)/growth irradiance (μmol m^{-2} s^{-1})			
	27/150	5/20	5/150	27/2200
PS II excitation pressure	low	low	high	high
($1-q_P$)	(0.1–0.2)		(0.7–0.75)	
Chl/Cell (fg)	730	716	130	180
Chl *a*/*b*	3.59	3.61	8.47	7.92
Photosynthetic capacity[a] (μmol O_2 mg Chl^{-1} h^{-1})	274	335	773	848

[a]The maximum photosynthetic capacity was measured at 27 °C.

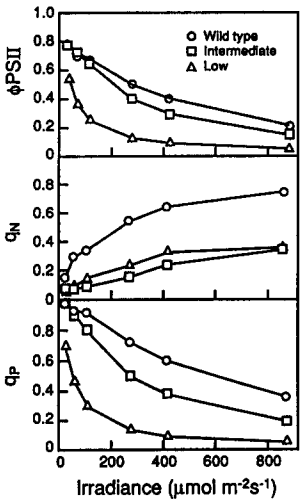

Fig. 3. Fluorescence parameters (øPS II, q_N and q_P) for wild type tobacco and two antisense Rieske FeS transformants (cf. Table 4) as a function of irradiance (redrawn from Price et al. 1995).

pressure, demonstrating these long-term acclimations to be of benefit under high light stress.

Maxwell et al. (1994, 1995) suggest that modulation of excitation pressure to PS II may be a critical component of a general signalling mechanism for all environmental stimuli, that initiates appropriate alterations to photosynthesis at the physiological, biochemical and molecular levels in response to fluctuations in environmental factors.

(ii) Chlorophyll b*-deficient mutants*

Chlorophyll *b*-deficient mutants have much higher PS II/PS I ratios than those of wild-type (Melis 1991). This response is appropriate since it will help to restore the balance of light absorbed between PS II and PS I and thus correct the mutation which attenuates the light-harvesting capacity of PS II. Interestingly, the Photosystem II stoichiometry of the chlorina Chl *b*-deficient barley mutant (PS II/PS I = 3) remained unaltered by growth in either PS I or PS II light, in marked contrast to wild-type (PS II/PS I in PS II light = 1.9; in PS I light = 2.7) (Kim et al. 1993a). Since changes in light quality in the Chl *b* mutants do not confer an advantage in the distribution of excitation energy between the photosystems, a cause-and-effect relationship occurs between the initial distribution of excitation energy and the ultimate PS II/PS I ratio. In this case, signal perception for the adjustment of photosystem stoichiometry suggests that photoaccessory pigments of the photosystems themselves act as light quality receptors, and that the photosystems play a role in signal transduction (Kim et al. 1993a).

(iii) Acclimation of antisense tobacco transgenics with lower amounts of the FeS Rieske protein mimics light acclimation

Tobacco transgenics with reduced amounts of cytochrome *b/f* complex were produced using antisense constructs generated from cDNA clones for the Rieske FeS protein (Price et al. 1995). Reductions in the amounts of the FeS apoprotein were directly proportional to decreases in maximum photosynthetic rates, and to the amounts of redox active Cyt *f* in leaves (Hope and Chow, unpublished) and cytochrome *f* apoprotein (Price et al. 1995). In accordance with their reduced capacity for electron transport due to diminished cytochrome *b/f* complex content, these antisense plants showed marked changes in composition and function. With increasing decline in Rieske FeS or Cyt *f* content on a chlorophyll basis (Table 4) there were smaller, but significant, declines in Chl *a*/*b* ratios

Table 4. Acclimation of sucrose-grown Rieske FeS antisense tobacco plants (Price et al. 1995)

Antisense phenotype	Chl *a/b*	Cyt f	PS II	PS I	PS II/PS I
		(mmol mol Chl^{-1})			
Wild-type	3.60	1.87	2.65	1.93	1.37
Intermediate	3.34	1.36	2.35	1.61	1.46
Low	3.23	0.24	2.20	1.45	1.52

(due to increases in both LHC II and LHC I), as well as in PS II and PS I reaction centre content. The PS II/PS I ratio increased slightly with increasing severity of the FeS loss (Table 4). Pmax and øPS II (the photochemical efficiency of PS II) were lowest in the most severe antisense plants at all irradiances (Fig. 3). Dramatic changes in q_N and q_P were also evident (Fig. 3). These profound changes in thylakoid composition elicited due to the change of one gene are reminiscent of acclimation to low light or shade in most respects. However, excitation pressure on PS II was *highest* in the most severe antisense plants; therefore, it would seem that excitation pressure on PS II acting as a transducer in PS II alone cannot explain the acclimation of the severe antisense plants.

Multiple feedback mechanisms from photosynthesis regulate chloroplast and nuclear gene expression for acclimation of the photosynthetic apparatus

The similarity of varied acclimation responses led to the proposal of a generalised regulatory mechanism for dynamic modulation of the photosynthetic apparatus by photosynthesis, in plants (Melis et al. 1985) and cyanobacteria (Fujita et al. 1987). These researchers initially identified the primary signal as the redox state of Cyt *f* or the plastoquinone pool, whereas others (Chow et al. 1990a; Kim et al. 1993a) suggested that the photosystems themselves act as primary sensors. Allen (1993) suggests that redox-regulated two component nuclear-encoded regulatory systems, similar to those in bacteria, may be involved, particularly to sense the redox poise of PS II and PS I and initiate cascades of kinase/phosphatase activities. Indeed, recently, interest has focussed on the redox state of Q_A (Huner et al. 1993; Maxwell et al. 1994, 1995), monitored as the excitation pressure on PS II ($1 - q_P$). While this idea is attractive for the interplay of irradiance and low temperature, it would not explain other effects: eg acclimation under long-term far-red supplementary light described earlier (Table 1), would lead to enhanced levels of oxidised components of PS II, plastoquinone pool and cytochrome b/f complex and ($1 - q_P$) would be expected to be diminished.

We suggest that signal transduction is mediated by mulitple mechanisms, rather than a common regulatory pathway (Fig. 4). Further, we suggest that PS II or PS I act as either (i) photoreceptors: regulatory light sensors for acclimation when photosystem function is affected directly by light (e.g. light quality), or as (ii) redox transducers, when alterations of the redox poise of the photosystems are involved in redox regulation. If so, the acclimation which occurs during growth in long-term supplementary far-red enhanced light (Chow et al. 1990a) could be explained by increased excitation pressure on PS I, as has been suggested for PS II by Maxwell et al. (1994, 1995). While a redox effect in electron transport monitored at any thylakoid complex will also be sensed at the other complexes, PS II complex is unique in that it monitors the flow of photons into PS II and the flow of electrons from Q_A, a factor vital for resistance to photoinhibition (Öquist et al. 1992a) and for the interplay of temperature and light acclimation (Maxwell et al. 1994, 1995).

Reducing power generated by PS I is also important in dynamic light regulation since reduced thioredoxin produced by the ferredoxin-thioredoxin system activates in the presence of light several key enzymes involved in carbon dioxide assimilation as well as ATP synthase (Buchanan 1994). In elegant research, Danon and Mayfield (1994) have shown that light also modulates a thioredoxin-mediated regulation of the translation of several chloroplast-encoded genes, particularly that of *psbA* mRNA which encodes for the rapidly turning-over D1 protein of PS II reaction centre heterodimer. Reduced thioredoxin reduces a regulatory

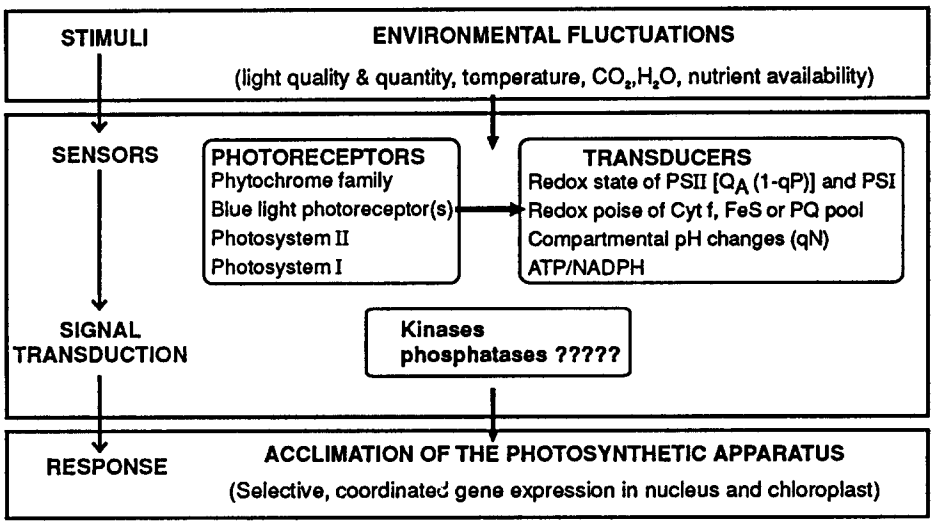

Fig. 4. Schematic of multiple feedback mechanisms from photosynthesis which influence gene expression during photosynthetic acclimation.

disulphide bond on the *psbA* mRNA-binding protein complex; this leads to an increased binding of the complex to the 5′-untranslated region of *psbA* mRNA and increases translation of several chloroplast-encoded proteins. This regulatory scheme is appealing because it provides a direct mechanism to couple the reducing power generated during photosynthetic electron transport to the regulation of translation of chloroplast-encoded genes.

The redox state of the plastoquinone pool or cytochrome *b/f* complex that reflects the redox poise between the functioning of the photosystems may also be the primary transducer in acclimation to light intensity. Indeed, evidence for chloroplast redox poise also influencing the transcription of a nuclear-encoded photosynthetic gene has been presented by Escoubas et al. (1995): transcription of the nuclear-encoded *cab* gene in the green alga, *Dunaliella tertiolecta* is reversibly repressed by a phosphorylated factor coupled to the redox status of plastoquinone through a protein kinase. This signalling system, which is yet to be tested in higher plants, uses LHC II as a photoreceptor: it allows direct feedback between photosynthetic electron transport and nuclear-encoded photosynthetic genes. In the short-term, finely-tuned control on LHC II via post-transcriptional protein phosphorylation allows the distribution of excitation energy to be balanced between the photosytems in state transitions. Under more sustained irradiance changes, longer-term coarse control over LHC II abundance is regulated by transcription.

It seems to us likely that *feedback mechanisms from photosynthesis relating to redox regulation can be monitored at several points* (Fig. 4). Multiple mechanisms for regulation would enable plants to distinguish between the opposing effects of different environmental cues.

Just as redox poise in feedback mechanisms of photosynthetic acclimation is important for the regulation of signal transduction arising from metabolic photosynthetic responses (Fig. 4), the redox poise of Q_A is central for the functionality of PS II and the opposing effects of photochemical ($1 - q_P$), and non-photochemical quenching in short- and long-term responses (Öquist et al. 1992a; Osmond 1994; Horton et al. 1994). Therefore, we suggest that it is important to consider not only photochemical quenching as excitation pressure on PS II or PS I as possibilities for signal transduction, but also the other side of the coin, long-term nonphotochemical quenching, q_N. In the short-term, q_N triggers non-photochemical dissipation of excess excitation by down-regulation of PS II (Osmond 1994; Horton et al. 1995). In the long-term, we suggest that increases in pH, elicited by photosynthesis in both the stroma and cytoplasm, will in turn modulate the contents and/or ratios of ATP/NADPH, and fine-tune the expression of nuclear and chloroplast genes.

Clearly many of the chains of specific processes that regulate acclimation of chloroplast components (Fig. 4) also control light energy dissipative processes, particularly of PS II, and both thereby act in synchrony

to maintain, if at all feasible, the balance between light energy supply and energy consumption under limiting, saturating and excess light. The grand design of photosynthesis with exquisite regulation ensures that the responses of both photoreceptors and Photosystems II and I, acting as their own light sensors, are inextricably linked with feedback metabolic responses from photosynthesis itself, which allow plants to respond to both sudden and sustained fluctuations in environmental cues.

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